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# PHYSIOLOGICAL PROBLEMS IN THE LIFE- HISTORIES OF ANIMALS WITH PAR- TICULAR REFERENCE TO THEIR SEASONAL APPEARANCE<sup>1</sup>

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## I. INTRODUCTION

THE fact that plants flower, fruits ripen, insects appear and disappear in succession throughout a growing season needs no statement even to the savage huntsman or the city flat dweller. The variations of the usual succession of appearances with peculiar seasons, unusual weather, etc., are general guides to many operations of primitive agriculture and matters of comment by all out of door people. Seasonal succession has long been scientifically investigated (see Alee, '11; Forbes, '16; Harvey, '08; Hough, '64; Johnstone, '08; Shelford, '13). Only recently has careful investigation of it been stimulated by the general interest in modern ecology and economic problems. The importance of a knowledge of delayed germination of seeds to the agriculturist (Crocker, '06) has further stimulated work along a line throwing light on the general subject. The analysis of the physiological causes of the normal succession of biological events in any season calls on many of the laws of biology to formulate merely the outline or even a portion of a life history, as, *e. g.*, the answers to questions such as why potato beetles appear from hibernation at a certain time, and not earlier, and deposit eggs on plants of the genus *Solanum*. Further, as soon as we concern ourselves with the analysis of the causes of the irregularities of appearance in any season, the evident complication of problems is such that one may

<sup>1</sup> Contribution from the Illinois Natural History Survey and from the Zoological Laboratory of the University of Illinois, No. 100.

undertake to discuss them without apology. The practical significance of variations to agriculture is shown by the destruction of the wheat crop in the Southwest by the wheat aphid. This was due to differences in response to weather on the part of the pest as compared with its enemies. The cause of seasonal appearance, or more especially of variations of seasonal appearance, is to be found in the influence of external factors on the initiation and velocity of growth and on fecundity and length of life, in dormancy in various stages in the life histories, and in the adjustment of the innate rhythm to the annual climatic cycle.

## II. THE INFLUENCE OF EXTERNAL CONDITIONS ON TIME OF APPEARANCE AND NUMBER OF INDIVIDUALS

1. *Differences in Initiation and Velocity of Development.*—The problem of initiation of development is one that has attracted much attention of late on account of the importance of an ability to predict the time when various insect pests will emerge from hibernation or will reach a stage of development at which it is necessary to spray, if such treatment is to prove satisfactory.

In this connection attention has been directed to the conditions, particularly of temperature, under which there is no development during periods lying within the bounds of the ordinary life history of the animal in question (Sanderson, '10, Headlee, and Peairs). The limit at which development does not take place, usually called physiological zero or zero of development, is better termed *threshold of development*. Sanderson has discussed various data and theories relative to the effect of temperature on development.

The attention of physiologists has been directed toward the study of the effects of temperature on the rate of metabolism and development. In general the results of such study have been interpreted with reference to Van't Hoff's law relative to the increase of reaction with a rise of temperature of 10 degrees, usually des-

ignated as  $Q_{10}$ .  $Vt$  is the velocity of development at any temperature ( $t$ ), so that  $Q_{10}$  is the quotient of  $\frac{V(t+10)}{Vt}$  and supposedly is a constant. In fact, the  $Q_{10}$  is not a constant for living phenomena, but usually varies from 2 to 3, being greater for the lower temperatures and smaller for the higher ones. Snyder has pointed out in detail that while the temperature coefficient for differences of 10 degrees varies, the variation is not only for physiological actions, but also for many chemical reactions; in both cases the variations are in the same direction. He finds that changes in viscosity with changes in temperature follow the same rule. He holds the hypothesis that even in the simpler physiological actions we have to deal with at least two distinct chemical actions whose fundamental velocities at any given temperature are different.

Recently Krogh ('14) has calculated the  $Q_{10}$  from  $Q_1$ ,  $Q_2$  and the like, at different temperatures for the time from fertilization of the frog's egg to the appearance of the first cleavage plane. He found 53.0 (published as 5.3, which appears to be a error) for the interval between 3 and 5 degrees, 4.1 for the interval 5 to 10 degrees, 2.0 for the interval 15 to 20 degrees. He raises the question as to the value of such a variable "constant." He calls attention to the fact that the velocity curve (the reciprocal of the time-temperature curve) is a straight line within certain limits. This is not the curve for the reciprocal of Van't Hoff's time and temperature formula. The latter law is valuable only as evidence that the life process is a combination of chemical processes. The condition of any environmental factor at which development does not take place, but immediately above which development may be initiated, is called the *threshold of development*. It is evident that there is a threshold of development for most species as regards temperature, moisture, light, oxygen, quantity and quality of food, and probably other factors. The brief state-

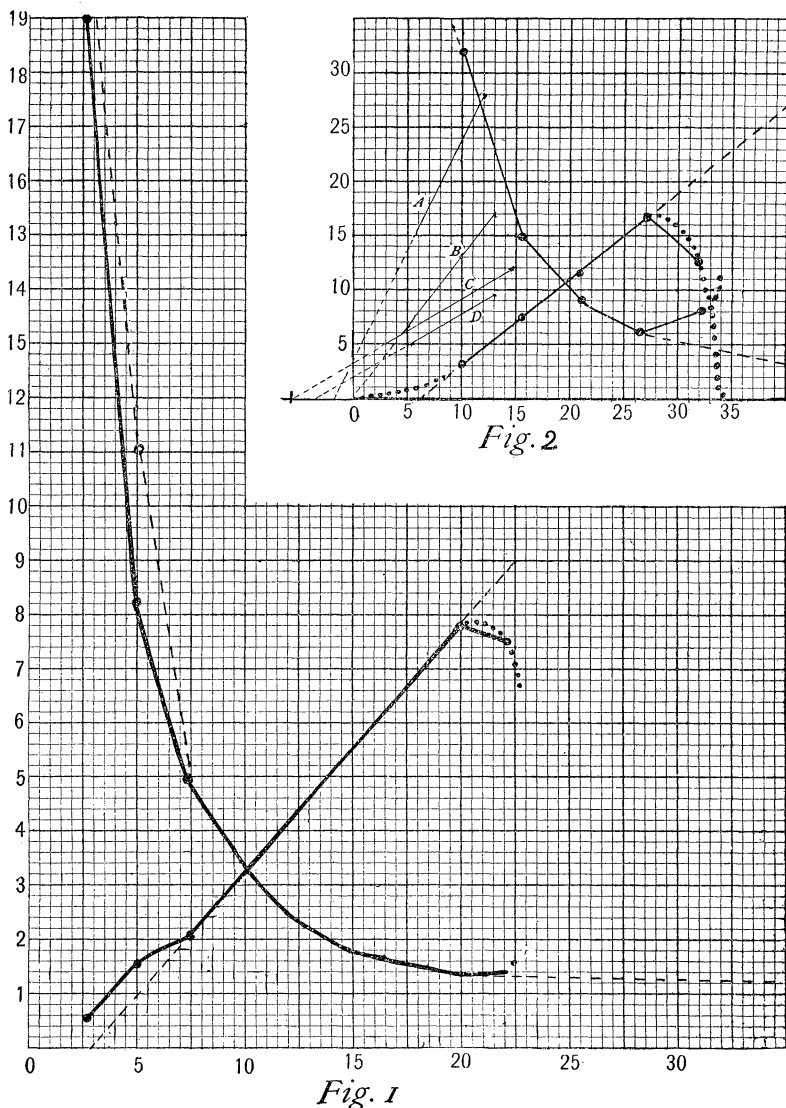


FIG. 1. Showing the time-temperature curve (the longer curve) for the appearance of the first cleavage plane in the egg of the frog. The solid curved line is the actual curve, and the broken line extensions are theoretical, based on the thermal constant ( $\text{time} \times \text{temperature}$ ) where it differs from the actual one. The shorter oblique curve is the velocity curve, or the reciprocal of the time-temperature curve, shown for the true hyperbola by the combined broken and solid lines of the longer curve. It is a straight line. The line of heavy dots shows the probable continuation of the curve based on Verworm's ('99, p. 397) irritability curve. The figures on the axis of abscissas are degrees Centigrade. The figures on the ordinates represent 100 minutes for the hyperbola and 100 divided by the time units for the reciprocal (from data by Krogh).

FIG. 2. Showing the time-temperature and velocity curves for the time from

ments and citations below are in support of this statement.

(a) *Temperature Threshold*

Very nearly at the time of the publication of Krogh's work, Sanderson and Peairs announced that for a large series of insects the time-temperature curve for development is a hyperbola and the velocity of development curve is a straight line. Peairs concluded further that the (reciprocal) relative velocity curve which is obtained by dividing unity (100 to avoid fractions) by the experimentally determined time periods, in days or other units, and plotting it against the temperature for which the time was observed, gives points for the different temperatures which fall in a straight line crossing the axis of temperature at the *zero* of the curve, or the theoretical threshold of development (Fig. 1). This theoretical threshold may be calculated also with two points accurately determined experimentally. These authors conclude that with the zero determined, the thermal constant (temperature multiplied by time—a constant for an hyperbola) can be obtained. However, they failed to note the deviations from law which occur at both high and low temperatures and which require careful attention in practical work.

These entomological workers appear to have overlooked the work of the fish culturists who have studied the subject of effects of temperature on development. Apstein ('11), Dannevig ('94), Earll ('78), Green ('70), Johansen and Krogh ('14), Reibisch ('02), and Williamson ('08) all made contributions of greater or less importance. All called attention to the effect of tempera-

birth to maturity of *Toxoptera graminum* (from Headlee after Sanderson and Peairs); the velocity curve represented by a heavy line is extended with dots to show the usual form of the irritability curve, and its mathematic extensions are shown as a heavy broken line. The light oblique lines are the velocity curves for the development of the eggs of four species of marine fish (after Krogh). *A*, the flounder (*Pleuronectes flesus*); *B*, the whiting (*Gadus merlangus*); *C*, the cod (*Gadus morrhua*); *D*, the plaice (*Pleuronectes platessa*). It will be noted that the mathematical zeros of development as indicated are at or below zero Centigrade and the rate of increase in development for each degree of rise of temperature is different for the different species and is indicated by the angle which the velocity curves make with the axes of the curves. The figures on the axis of abscissas represent degrees Centigrade. The figures on the axis of ordinates are days for the hyperbola and 100 divided by days for its reciprocal.

ture on the rate of fish development, particularly during the late embryonic stages. Reibisch ('02) showed that  $\text{time} \times \text{temperature}$  is a constant, using the hyperbola. He called the temperature at which development could be initiated by the slightest increase the "*threshold temperature*," which is the same as the zero of development and physiological zero of other authors. He calculated this from the hyperbola formula, thus anticipating the work of Sanderson and Peairs by about eleven years. In fact, the idea of ineffective temperature below a minimum and a sum of temperatures which is the product of  $\text{time} \times \text{temperature}$  dates from de Candolle's 1830 article.

Johansen and Krogh worked over the data of Dannevig and showed that the velocity is different for different fishes (Fig. 2, *A, B, C*). They note further that temperature is not absorbed by the organism and that the constant is only a convenience. They call attention to the fact that the velocity-of-development curve is a straight line which, prolonged downward, crosses the axis of abscissas at a point mathematically corresponding to Reibisch's threshold temperature. The threshold of development would be where the velocity curve crosses the axis of abscissas if the straight-line velocity curve held good and the time-temperature curve were a true hyperbola. Krogh ('14) showed that while 2.7 degrees is the mathematical threshold of development for cleavage of the frog's egg, the first cleavage appeared at this temperature 1,844 minutes after fertilization. If the curve were an hyperbola, at 2.7 degrees the development of the cleavage plane should have required an indefinitely long time; or, in other words, it should not have appeared at all. Also, at 4.9 degrees the appearance of the cleavage plane should have required 1,100 minutes, while the observed time was approximately 730 minutes. Further, it required 138 minutes for the cleavage furrow to appear at 22.1 degrees, which is more than at 20.7 degrees, showing a decrease in velocity at higher temperatures. Thus Krogh points out that the velocity curve is a straight line only between 7

and 21 degrees, while the limit of development is from less than 3 to 22.1.

Thus comparing the velocity curves for Headlee's development of *Toxoptera* (Fig. 1) and for the cleavage of the frog's egg, we note that in the case of the frog's egg the velocity is too great at the lower temperatures and falls off at the highest temperature. Also, in the case of Headlee's curve for *Toxoptera*, the development was much too slow at the higher temperatures. Krogh ('14) further studied the development of pupæ of *Tenebrio molitor*, carefully measuring the carbon dioxide given off. He found that the curve of velocity was a straight line between 18.5 and 28 degrees, but that it curved upward at lower temperatures. He tried incubating the pupæ at 13.45 degrees, which is the mathematical zero of his curve, and found that they developed in 1,116 hours, but with considerable mortality. At approximately 33 degrees the velocity was less than it should be if the curve were a true hyperbola. An interesting feature of these curves is that they approach so nearly to the curve published by Verworn showing the stimulation effect of heat on activity. This curve is shown in Fig. 2 by the actual velocity curve and the dotted extensions which, when compared with the curve of Krogh for the development of *Strongylocentrotus*, *Arbacia*, and *Tenebrio*, indicate the close relation between the amount and rate of activity and that of general metabolism and growth.

Edwards ('02) made a careful study of the hen's egg and established 20–21° C. as the point at which no development takes place. There is an optimum temperature and development is accelerated by slightly higher temperatures and retarded by lower temperatures. Thus even in a warm-blooded species there is a point at and below which development does not occur.

#### (b) *Prediction on the Basis of Temperature Laws*

Can we predict the time of appearance of any stage in the life cycle of an animal? Certainly, in so far as we



are concerned only with temperature and with temperatures within the straight-line limits of the velocity curve, we can predict with a high degree of accuracy the time at which any stage will be reached. Further, within the

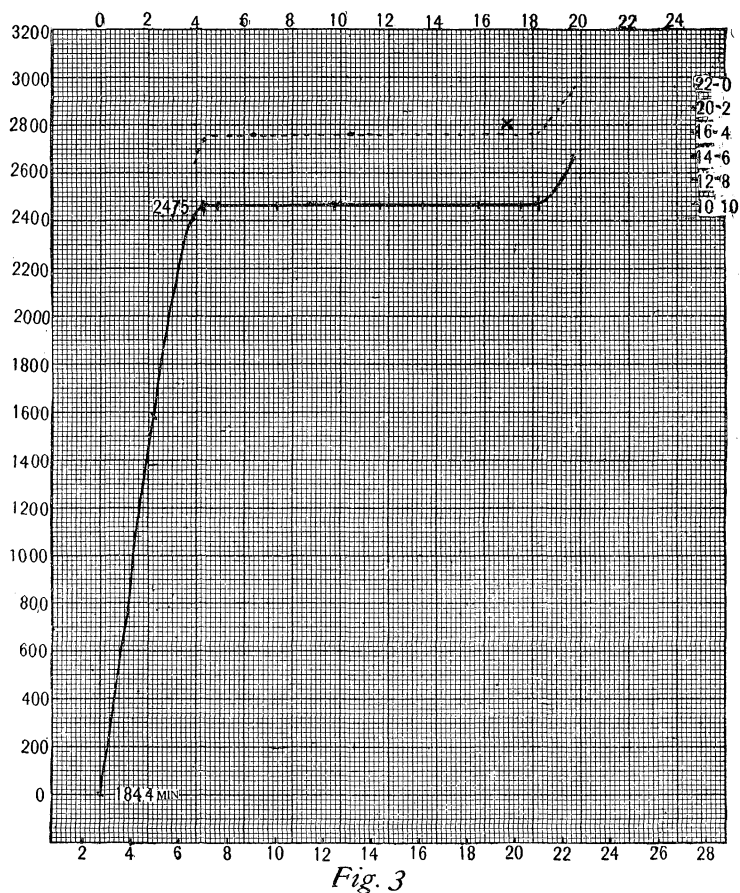


Fig. 3

FIG. 3. Showing the total temperature curve for the appearance of the first cleavage furrow in the egg of the European frog, as a continuous line from the data of Krogh. The small cross dashes show the temperature at which experiments were performed. The actual temperatures are given at the bottom of figure; at the top the actual degrees above the theoretical threshold of development, which is 2.7 degrees C. The figures at the left show the total minute-degrees, time  $\times$  temperature, which range from zero on the scale to 3200. At the right is shown a scale for different degrees of light; these figures are added to illustrate a method of chart-making only. 10 units of light are assumed to give quickest development, and both increases and decreases, to give slower development and hence more time-temperature units, as suggested by the broken line above the main curve. The cross shows approximately what the total time-temperature would be if darkness slowed the formation of the cleavage furrow in the same manner as it slowed general development during an entire month in the experiments of Yung. For further explanation see text.

straight-line limits the effects of constant and variable temperatures should be the same. This is due to the fact that the product of time units  $\times$  temperature above the threshold of development is a constant within the straight line limits. Where it is not a constant, the actual values may be plotted approximately for any temperature.

Using the data of Krogh (Fig. 3), I have drawn an approximate total temperature curve for the development of the first cleavage plane for the egg of the frog. The number of degree-minutes required for completion of the cleavage furrow is the same for all temperatures between  $7^{\circ}$  and  $21^{\circ}$  C. That is time  $\times$  temperature is constant between  $7^{\circ}$  and  $21^{\circ}$  C., where it is about 2,475 time-temperature units or minute-degrees, and the curve is a straight line. Above 21 degrees the total temperature is greater than the constant, and below the lower limit of the constant it is less than the constant. At 2.7 degrees it should be infinity if the hyperbola held good, but is actually 1,844 minutes. The time-temperature units are not expressible at this point, so the actual time is given. If development takes place below the zero of the hyperbola, the time-temperature units may be considered as having a negative value, but are expressible. From this curve it is possible to tell how long it takes for the cleavage furrow to develop at any temperature shown; for example, take 6 degrees (bottom of chart = 3.3 degrees at top). We find from the curve that the total temperature for this is approximately 2,200 degree-minutes. Thus, 2,200 divided by  $6.0 - 2.7$  gives 666 minutes. It is true that the same result could be obtained by reading off the time on a time-temperature curve (near to hyperbola) with less labor, but the region in which the total temperature is a constant cannot be shown on such a curve; and the time for different temperatures is obtained with less simple calculations from the reciprocal. The total temperature curve exaggerates the straight-line limits, and brings out sharply the fact that high temperatures retard and low temperatures accelerate as compared with the veloci-

ties indicated by the reciprocal of the hyperbola to which the data partially conform.

Factors other than temperature influence the rate of development. The work of Yung showed that in the case of the frog light is one of these. Unfortunately the light was not measured definitely in the work of either Krogh or Yung. Yung kept one lot of developing frogs in the dark and one in a window but where the sun actually never shone on them. Krogh's work must have been done in similar light. Yung's larvæ were reared under the light conditions which he used, for a month or two months, and thus his data are for older stages than those of Krogh, whose results relate to the appearance of the first cleavage furrow. Accordingly, any comparison of the two sets of data is essentially impossible. However, for the purpose of illustrating a principle which is indicated relative to development under the influence of various intensities of factors other than temperature, I have called the light condition under which Krogh's work was done 10 units and have shown it on a scale at the right-hand side of the graph. It is probable that too strong light will retard development as well as too weak light. Hence the scale is shown double, 12-8, 14-6, etc.; either increases or decreases in light intensity are assumed to increase the time required for development. The cross shown on the graph gives the approximate total temperature for darkness indicated by Yung's work. This part of the chart is given merely to indicate a method of chart making—of showing the way in which variations of one other factor change the number of time-temperature units required for development.

For practical prediction such a curve must be drawn for the shortest time for development at each temperature. This will be under optimum light, chemical, etc., conditions for the temperature concerned. In establishing such a least-total temperature curve a few careful determinations within the straight-line limits with other factors optimum will suffice. Outside these limits the de-

terminations must be more numerous and especial care must be exercised to have the temperatures constant. In determining the optimum light for different temperature much more rapid progress can be made by running experiments under at least three conditions of this factor for each temperature. Deviations due to factors other than temperature should be shown on such a chart probably in a manner indicated by the broken line on Fig. 3. If the main curve is drawn for shortest time, all deviations in light, etc., will *increase* the so-called total temperature, and lines may be drawn for these conditions above the main curve as the facts necessitate.

Much investigation will be necessary to determine the corrections which must be made in determining *mean* temperatures which must be derived from conditions in which the temperature slowly rises and falls during several hours of each day, within the ranges of temperature where the velocity curve is not a straight line. Temperatures outside the straight-line limits should not be mixed with the temperatures of the straight line limits. These outside temperatures must be considered or estimated in terms of units sufficiently small to approach accuracy. In the case of daily temperature fluctuations the temperatures outside the straight-line limits must be considered by hours, and suitable corrections made before they can be included in the daily mean. The exact nature of this correction will have to be determined by careful investigation.

#### (d) *Humidity Threshold*

The workers thus far cited have studied temperature alone, intending in a general way to keep other factors constant. There is undoubtedly a threshold of development with reference to each factor which influences development. Berger found that growth ceased in tenebrionid larvæ fed on bran dried at 105 degrees, and that they lived for months with a loss of weight; doubtless with a very small increase in moisture they could be maintained at the initial weight. More recently Pierce has found

that the cotton boll-weevil has a different zero or threshold of development and different temperature optimum for each humidity.

(e) *Oxygen Threshold*

The development of various invertebrates is stopped by insufficient oxygen (Loeb, '06, and citations). Johansen and Krogh found that if the oxygen pressure was reduced to one half by reducing the air pressure to 380 mm. of mercury development of plaice eggs was retarded. The oxygen pressure threshold of development lies below the amount which will go into solution from air at pressure of 230 mm. of mercury, but at this concentration much care was necessary to keep the eggs alive. Shull ('11) determined the oxygen minimum for the germination of the seeds of *Xanthium*.

(f) *Light Threshold*

Loeb ('11) states further that light is necessary to the regeneration of zoids in *Eudendrium*. Its absence is further known to slow development in larvæ of insects which normally live in the light (Bachmetjew, 692). Smith found that light accelerates the development of salmon. Johansen and Krogh found little difference between marine fishes grown in light or in dark. Davenport ('99) summarized the literature to that date and showed on the authority of Yung that moderately strong light increased growth.

(g) *Food Threshold*

Recent work has shown that food may be either qualitatively or quantitatively deficient and cause standstill in the development of mammals. Thus Osborne and Mendel (p. 101) show the following methods of producing it:

(1) By under-feeding with rations of suitable qualitative make-up; (2) by the use of diets containing an adequate protein but with inorganic salts supplied in the form of a mixture of pure chemicals together with sucrose and starch as the carbohydrate component; (3) by restricting

the protein content of the dietary below the minimum required for growth; (4) by furnishing as the exclusive source of nitrogenous intake proteins which lack some amino-acid group indispensable to growth.

Thus the animals were maintained at practically the same weight and they retained their power to grow long past the age at which growth normally ceases (335 days) and for periods equal to half the normal life of the species, which is 1,000 days.

Wodsdalek ('17) has shown that certain tenebrionid larvæ can not only be maintained, but may be reduced from half-grown to hatching size several times by repeated starving and feeding. This seems to leave little doubt as to the existence of a threshold of development for food.

#### (h) *Definite Amount of Development*

Krogh has shown that the total amount of carbon dioxide given off by pupæ of *Tenebrio molitor* is the same for all temperatures, showing that there is a definite amount of development to be attained. The rate appears to be different for different species where no considerable difference in the total for passing the stage in question is to be expected, as in the case of fishes (see graphs by Krogh). Thus, difference in velocity and increase in velocity at different temperatures and moistures, etc., have an important bearing on the variable or unequal seasonal appearance of the different species. The acceleration of development under conditions of factors near the threshold is a further consideration (for a noteworthy instance see Bachmetjew's ('07) retabulation of Merrifield's ('90) data) which leads to non-coincident appearance and peculiar modification of normal sequence in abnormal seasons.

It appears that the chief reason that there are not more generations in an annual cycle in the case of spiders or other animals is that the amount of energy which must be expended and the velocity of development are such

that the completed sexually mature individual can not be produced oftener than usually obtains. There is, to be sure, much evidence that the tendency to hibernate is not very firmly established in some species and that under stimulation animals may be induced to reproduce nearly continuously, at least for a number of generations. Cessation of development in any given case is as much attributable to some factor falling below the threshold of development as to heredity. The environment is extremely complex, and the number of factors which may cause cessation of development and which have been already established, are so numerous as to indicate that the number is very much greater than is commonly supposed, including temperature, moisture, light, oxygen, evaporation, quantity of food, or absence of any one of many necessary food constituents. These appear to operate in accordance with the law of toleration (Shelford, '13) and, with respect to food, in accord with Leibig's law of minimum. Where dormant periods are well established, their occurrence with reference to the usual seasonal rhythm makes any modification of the usual life history difficult or impossible.

Variations from the "normal" seasonal weather, and weather changes are of especial interest as modifying the usual seasonal succession of adult animals or any area. In springs with unusually prolonged cool weather, the various pond species, such, for example, as those noted on page 146, are crowded together, and reach maturity much more nearly at the same time than in normal seasons. The same phenomenon has been observed by the writer in the case of the flowering of early spring plants of an area near Chicago. The differences in the response of different species to the same conditions show their different physiological constitutions. This type of variation indicates that such maladjustments as resulted in the depletion of the grain crop by the grain aphid in the southern part of the wheat belt, because the weather favored them, may occur in undisturbed localities, though

probably not to the same degree. Seasonal succession and its variation involve, for the pure-science student, many of the problems which confront the economic zoologist.

3. *Length of Life and Fecundity*.—One phenomenon which has been repeatedly noted in connection with this study—a matter of common observation—is the variation in numbers of individuals in different years. The length of life of individuals may have a pronounced effect on the population and succession of species on a given area. Loeb has stated that the great number of individuals in the plankton of the polar seas in summer is due to the longer life of the individual at low temperature. Unless the low temperature slows the different processes unequally this can hardly follow. For example, if a parthenogenetic female aphid normally lives a week and produces 1,000 offspring and then the temperature is lowered so as to prolong the life to three weeks, unless the different functions were unequally affected by the change, there would be at the end of three weeks but a thousand, while at the normal rate there would have been a billion possible individuals. On the other hand, if the rate of reproduction remains the same and the length of life of the individual after the reproductive period is increased, the results of lower temperature would be very different, perhaps much as Loeb assumes. Actual observations along this line are few. In the case of the San José scale, however, Glenn ('15) found that the number of offspring is greatest in the individuals breeding in the warmest weather. Turning to Table I we note (page 146) that *Agelena nevea* may live longer in the adult stage than *Argiope aurantia*, or the time of appearance may be more irregular, and hence the question is one for investigation.

The velocity of development of different species is different, and the relative velocity is measurable in some terms of the angle which the velocity curve makes with the axis of abscissas (Fig. 2). Thus when we compare the four species of fish given by Dannevig we note that



velocity of development increases more rapidly with increases of temperature for the flounder than for the plaice; the same difference exists between the whiting and the cod. Krogh showed that the velocities of the different stages of the frog's egg, Fig. 1, are the same; but the different stages in the life history of the same animal may differ in velocity at the same temperature.

4. *Dormancy*.—Dormancy is of much importance among animals inhabiting the same area. Thus the eggs of *Eubranchipus* and *Diaptomus stagnalis* require both summer drying and winter freezing before they will hatch. Dormancy is common in the eggs of grasshoppers (Thomas, '79), walking sticks (Trouvelot), etc. Dormant periods are common, occurring even in deer and armadillo embryos (Patterson), and probably represent hereditary remnants of impressions made on former generations by seasonal rhythms.

The causes of these rhythms often are simple. Concerning delayed germination or dormancy of seeds, Crocker and Davis ('14) have said:

The work to date has shown that delayed germination of seeds is secured in a variety of ways: by almost absolute exclusion of water by seed coats (as in the hard-seeded legumes and species of several other families), by the limiting of the degree of swelling of the embryo, . . . by reduction of oxygen supply below the minimum for germination . . .; and finally perhaps by deficiency in salts. To this must be added delays due to embryo characters.

Dormancy has been overcome by drying in the case of several species of insects in the writer's laboratory.

### III. SEASONAL SUCCESSION AS ILLUSTRATED BY THE SPIDERS OF A SMALL AREA OF GROUND

In the spring and summer of 1910, Mr. G. D. Allen undertook the study of the seasonal succession of the fauna of an area in a vacant lot at Eighty-first Street and Blackstone Avenue, Chicago, which is a pond in spring and low prairie in summer, but did not complete the work, though his collections were extensive and thorough, extending

from the middle of June to November. Miss Katherine Norcross arranged the records in seasonal order, except those of the spiders. In the case of the insects which made up the vast majority of species on such an area, the question constantly arose as to where the insect had been previous to its appearance there. During the spring and summer of 1913, the writer undertook to collect and observe the spiders of the plot studied by Allen. Spiders were selected for this study because they do not undergo a metamorphosis, and may often be found and identified in a juvenile condition while insects can not. Though incomplete, the data are adequate for a discussion of the physiological features of seasonal succession.

The habitat from which the specimens were collected was about  $25 \times 50$  ft., nearly all of it covered with water in early spring, usually drying during May, and containing water thereafter only during and after especially heavy rains. In July Allen found the vegetation composed chiefly of *Eleocharis*, *Spartina*, *Carex*, *Juncus*, *Liatris*, *Steironema*, *Cacalia*, and several other composites. The plants taken together made up what is commonly called coarse grass and weeds. The writer's collections in 1913 were made on or very near Allen's dates for 1910. From these joint sources the data of the following table were obtained and arranged, but with some gaps where the spiders were probably too young to identify. The records marked "C" are taken from Comstock ('11) and represent the conditions in which the spiders usually are at the dates indicated. The spiders were identified by Banks ('10) and the nomenclature is according to his list.

1. *Statement of Succession*.—In the spring the area is a pond in which various Crustacea and worms succeed each other (see Shelford, '13, pp. 278). Sexually mature adults appeared in abundance about as follows: *Amblystoma tigrinum*, March 15; *Eubranchipus*, April 15; *Planaria velata*, May 1; *Diaptomus stagnalis*, May 1. Some of these animals have been studied sufficiently to show that they become dormant for the remainder of the year

as soon as the pond dries up. *Amblystoma tigrinum* deposits its eggs and then burrows into the mud and remains ten months in estivation and hibernation. *Eubbranchipus* deposits eggs that must be both dried and frozen before hatching. *Diaptomus stagnalis* is similar in character. *Planaria velata* forms cysts which live over to the following spring.

TABLE I

SHOWING SEASONAL SUCCESSION OF ADULT SPIDERS ON A LOW PRAIRIE SUMMER DRY POND

The species are arranged in the order of the seasonal occurrence of adults. \* indicates adults; *j*, young; *e*, eggs; *g*, generic identification only. *C* indicates that the occurrence is creditable to Comstock and is not based upon the author's observation. Dates are given at the heads of the columns in numerals only.

	4-30	5-6	5-22	5-26	7-10	7-24	8-6	9-6	9-30	10-12	11-6	Adult Weight in Gg.
	1	2	3	4	5	6	7	8	9	10	11	
<i>Pardosa modica</i> Blck.....	*	*	*									
<i>Tetragnatha laboriosa</i> Htz.....	<i>gj</i>	*	...	*	...	* <i>j</i>	*	<i>j</i>	...	<i>j</i>	...	.....
<i>Xysticus gulosus</i> Key.....	<i>gj</i>	*	...	...	...	...	...	*	*	<i>j</i>	<i>j</i>	.....
<i>Dictyna sublata</i> Htz.....	...	*	*	*	...	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	...	.....
<i>Pisaurina undata</i> Htz.....	...	*	...	...	...	* <i>j</i>	* <i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	...	300
<i>Attus palustris</i> Peck.....	...	*	...	*	...	...	*	...	...	...	...	.....
<i>Pardosa canadensis</i> Blck.....	<i>gj</i>	<i>j</i>	<i>j</i>	*	*	...	...	...	...	...	...	.....
<i>Lycosa heluo</i> Wal.....	...	...	...	*	*	...	...	*	...	...	...	.....
<i>Phidippus podagrosus</i> Htz....	<i>j</i>	<i>j</i>	<i>j</i>	* <i>j</i>	*	*	<i>j</i>	<i>j</i>	...	<i>j</i>	...	200
<i>Plectana stellata</i> Htz.....	...	...	...	* <i>j</i>	...	...	*	*	*	...	...	25
<i>Epeira trivittata</i> Key.....	...	...	...	...	*	...	...	*	...	...	...	.....
<i>Runcinia aleatoria</i> Htz.....	...	...	...	...	<i>j</i>	*	*	*	...	...	...	160
<i>Mangora gibberosa</i> Htz.....	...	...	...	...	...	* <i>C</i>	*	*	...	...	...	.....
<i>Agelena nivea</i> Wal.....	...	...	<i>jC</i>	<i>j</i>	<i>j</i>	*	*	*	*	*	<i>eC</i>	80
<i>Misumessus asperatus</i> Htz....	...	...	...	<i>j</i>	<i>j</i>	<i>j</i>	* <i>j</i>	...	...	...	...	.....
<i>Phidippus audax</i> Htz.....	<i>jC</i>	<i>jC</i>	<i>jC</i>	<i>jC</i>	<i>jC</i>	<i>jC</i>	*	* <i>j</i>	* <i>jC</i>	<i>jC</i>	<i>jC</i>	80
<i>Argiope aurantia</i> Luc.....	<i>jC</i>	<i>jC</i>	<i>jC</i>	<i>jC</i>	<i>jC</i>	<i>jC</i>	*	*	*	<i>jC</i>	<i>jC</i>	.....
<i>Argiope trifasciata</i> Forsk.....	<i>jC</i>	<i>jC</i>	<i>j</i>	<i>j</i>	<i>j</i>	<i>j</i>	*	*	*	<i>eC</i>	<i>jC</i>	425

At the time these appear, land animals begin to move about the pond margin, adult and juvenile spiders among them. The collection and arrangement of the entire fauna showed the same thing as the spiders, but proved much less satisfactory in the other cases than was expected, owing to a lack of knowledge of life histories and an inability to identify young stages. Turning to Table I and following out the stars which indicate the occur-

rence of adults, and noting that the species have been arranged in the seasonal order, starting with *Pardosa modica* Beck, which was taken only in April, we end the season with adult *Argiope trifasciata*, which appeared as adults late in the season only.

We note that when the collection proved at all complete the juvenile individuals follow the adults of the early spring species, and that they both precede and follow the species which mature late in the season. The collections proved to have been made with insufficient detail, and many young spiders could be identified only to the genus and are usually omitted entirely. However, the tables show a sufficient general arrangement of the species throughout a season to furnish an adequate basis for a discussion of the problems involved in the phenomenon of seasonal succession—the problems presented by a comparison of the few species whose life histories are known quite completely.

#### IV. DISCUSSION

Nearly all species are adjusted to the seasonal rhythm of the habitat in which they live. Thus *Dyctyna sublata* appears as adult in May and June, when, as it seems, eggs must be laid, and juvenile forms characterize the late summer and autumn. *Argiope trifasciata* deposit eggs in October and passes the winter in the juvenile form. *Phidippus podagrosus* reaches maturity in July, when eggs must be deposited, and young occur in both fall and spring. These differences generally represent an innate adjustment of the life cycle to seasonal rhythm, not readily broken up. It is to be expected, then, that *Dictyna* will deposit eggs to better advantage and that the young hatch better in May than in November, as is the case of *Agelena nivea*. It is further to be expected that the young stages of some spiders will not go on with development until cooled for a considerable period. Perhaps one of the most interesting questions concerning the whole matter of succession of spiders is to be found in the fact that from what is known about them, they are all active

for about the same period of time; *i. e.*, all life histories involve about the same period of activity and rest.

An inspection of the table shows that the time of reaching the adult stage varies for the different species, so that there is a general change of spiders in the adult stage as the season progresses. This is all that seasonal succession can mean under any conditions; the fact that the eggs or other young stages can not be identified or their location is unknown does not change the character of phenomenon in any locality where the species are resident.

The causes of the succession of species may be roughly summarized as follows: Species differ in the time in the annual climatic rhythm at which development begins, in the time of occurrence of dormancy and in the conditions necessary to break it up, in threshold of development relative to several climatic factors, in velocity of development relative to several climatic factors, food, etc., and in size and total energy expended. These may be taken up one at a time.

Considering differences in the time in the annual cycle at which development begins, as a factor in seasonal succession, we must notice first that this can be a controlling factor only where there is no dormancy in the life history or where the available total of temperature, moisture, light, etc., above the thresholds is just enough to produce one generation per year and not to permit of a gradual moving of the time of appearance to an earlier date each season, during several successive long seasons. The test of this would come in the migration of agricultural pests which are arrivals in localities where the growing season is longer. There appear to be no easily available facts, and for the present this type of maintaining a definite time of appearance is to be regarded as a theoretical possibility. The fact that the life histories of various animals which have been known to migrate extensively into new territory appear not to be accelerated indicates that dormancy may control appearance and thus time of beginning development may be a secondary consideration.

Thus we come to the time of occurrence of dormancy and the conditions necessary to break it up, which result in the rhythmic tendency of the species fitting into the rhythm of the climate in which it lives. In many insect species it appears that drying may be substituted for freezing. Such species may migrate into climates in which there is a dry season, instead of a cold one, and with a longer growing season, and continue with the usual annual life-history rhythm. Under these conditions in each growing season the development is stopped by dormancy and proceeds no further until the drying breaks up dormancy. The development of *Eubbranchipus*, once initiated, proceeds until the mature individual has produced eggs. Here dormancy stops all further progress until the eggs are first dried and then frozen and warmed above  $0^{\circ}$  C. Crustacea without dormant periods go on developing and produce several generations in one summer. After the conditions necessary for the overcoming of the dormancy have been fulfilled, or where there is no dormancy, species differ in the threshold conditions for development. The thresholds for development are hardly the same for any two species in which thresholds have been determined. Thus species will differ in the time at which development is initiated in the spring. Further, the increase in velocity with increase in temperature is different for different species, as indicated by the differences in the angle which their velocity curves make with the axis of abscissas (see Krogh, '14, velocity curves of several species of fish, also Fig. 2). This fact alone makes it possible for a given set of conditions out of the ordinary to give a peculiar and irregular occurrence of the different species of a community.

The total energy as illustrated by the  $\text{CO}_2$  given off by a species is the same for all conditions in which development can occur at all, as shown by Krogh. It is probable, accordingly, that the total energy expended in development is different for each different species. This may bear some relation to size and weight, though alcoholic

specimens of full-grown females of several species of spiders were weighed and no conclusion could be drawn. Either the method of obtaining the data or the fact that the spiders are all annual is the cause. Krogh found that the velocity of development is the same at the same temperature in the different stages of the frog, though the thresholds are different. But there is no reason to assume that this is true of other animals, especially where there is a metamorphosis.

1. *Conclusions.*—The preceding pages indicate the intricacy of the problems involved in explaining the simplest life history of annual animals. The physiological life histories of animals which have two or more generations per year, and of those whose life cycle extends over more than one year, are still more difficult to deal with. The problems involved have of late attracted the interest of biologists generally, of geneticists, of economic entomologists, of fish culturists, and others, and they constitute a central group of problems for the ecologist. All these various interests are being focused on the problems of physiological life histories as the next step in the attempt to advance the science of biology. In all these lines, the day of the naturalist taxonomist as a central figure is all but past, and the day of the naturalist physiologist is at hand.

This interest has arisen in the various groups for different causes, but one of them is the variation which occurs in the succession of species and their interaction in different years, due to peculiar weather conditions. The green bugs destroyed the wheat crop in 1907 because of differences in thresholds of development of the aphid pests and their enemies; the fruit growers do not spray at the right time in many cases because the insect pests do not appear at the usual time. This is not to be credited to the effects of one factor alone; as, for example, enough work with temperature has been done to show that, while it is important, the influence of other factors is sufficient to make prediction on the basis of temperature alone quite unreliable.

The animal geographer is interested in the same problems. We note that the animal community illustrated by the spiders contained animals maturing at every season of the year. There is a noticeable early spring or vernal group which the geographer has assumed is montane in origin (Adams, '09); and the group of land species which appears through the summer is traced into different situations according to specific affinities. It is evident that successful species are those that fit into the seasonal rhythm with respect to physical conditions, food, and numerous other relations.

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